

On the length of the internodes in the sciatic nerve of *Rana temporaria* (Fusca) and *Rana pipiens* : being a re-examination by biometric methods of the data studied by Boycott ('04) and Takahashi ('08) / Shinkishi Hatai.

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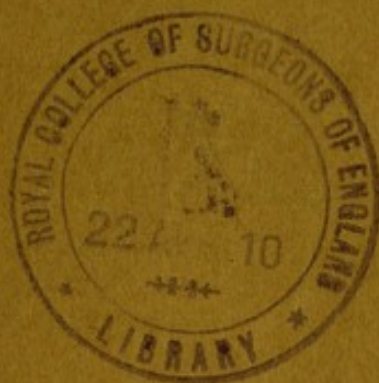
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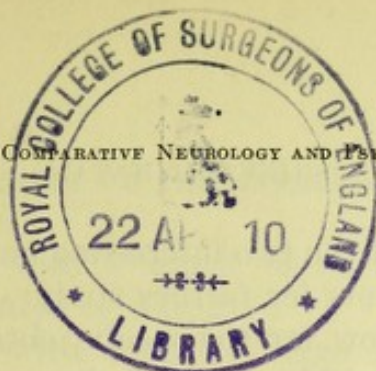
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ON THE LENGTH OF THE INTERNODES IN THE
SCIATIC NERVE OF RANA TEMPORARIA (FUSCA)
AND RANA PIPIENS: BEING A RE-EXAMINATION
BY BIOMETRIC METHODS OF THE DATA STUDIED
BY BOYCOTT ('04) AND TAKAHASHI ('08)

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WITH THREE FIGURES

In 1904 Boycott published an important paper on the length of the internodes under the title "On the number of nodes of Ranvier in different stages of the growth of nerve fibers in the frog." In this work he measured 5338 internodes from twenty-six frogs which ranged in body length from 14.5 mm. to 53.9 mm. Although his observations were limited to the fibers from the thigh taken at the division of the sciatic nerve into the n. tibialis and n. peroneus, they nevertheless give us definite information as to the lengthening of the internodes first in relation to the lengthening of the leg, and second in relation to the increase of the fibers in diameter.

Four years later (1908) Takahashi published a paper on the same subject under the title "Some conditions which determine the length of the internodes found on the nerve fibers of the leopard frog, *Rana pipiens*," and in this investigation he examined several new points. Takahashi's observations were made not only at three different levels in the thigh, but also at levels in the shank and in the foot, as well as on some of the spinal nerve roots.

He measured altogether 3068 internodes from eight frogs mostly of a larger size than those used by Boycott. The body lengths of Takahashi's specimens ranged from 39.0 mm. to 89.4 mm.

The examination of the two interesting papers just mentioned, suggested several points for further study. It seemed desirable to determine first, how far the results obtained by the simple method of averages would agree with those obtained by the more elaborate statistical treatment of the data; and second, whether or not there is some definite law expressing the relation between the length of the internode and diameter of the fiber on which it occurs, both in different segments of the leg of the same frog, as well as on the same segment of the leg in frogs of different sizes.

In order to investigate the problems just mentioned, it was necessary to reexamine the original data used in the foregoing researches, and through the efforts of Prof. H. H. Donaldson, I was so fortunate as to get the generous permission of both Boycott and Takahashi to use their valuable original data for this investigation, and I wish to express here my thanks to all of these gentlemen.

METHOD OF TREATING THE DATA

As has been shown by Boycott and Takahashi, the length of the internode is highly variable, even on the same fiber, as well as on fibers of the same diameter, and therefore in order to get proper mean values in the case of Boycott's records, I have combined the data for several frogs, and out of the total of twenty-five frogs, made five groups according to the length of the sciatic nerve as determined by Boycott.¹

Group 1. Those with a sciatic nerve measuring from 15.5 mm. to 17.0 mm.: represented by 2 frogs.

Group 2. Those with a sciatic nerve measuring from 20.0 mm. to 22.5 mm.: represented by 7 frogs.

Group 3. Those with a sciatic nerve measuring from 24.0 mm. to 26.5 mm.: represented by 6 frogs.

¹ The length of the sciatic nerve as defined by Boycott is the distance from the point of emergence from the vertebræ of the upper of the two larger branches of the plexus to the level of the nerve obtained by cutting across the leg through the knee joint when it is in full extension; *loc. cit.*, p. 371.

Group 4. Those with a sciatic nerve measuring from 30.5 to 37.0 mm.: represented by 4 frogs.

Group 5. Those with a sciatic nerve measuring from 46.0 mm. to 53.5 mm.: represented by 6 frogs.

In the case of Takahashi's data, I found that the internodes had been measured at the lower end of the thigh in only four frogs, giving a total of 683 measurements. These frogs moreover differ so widely in body weight that the data are insufficient for biometric treatment. For this reason I have decided to analyze Boycott's data as completely as possible and then merely to compare the results obtained with Takahashi's conclusions.

I shall present my results in the following order:

I. A confirmation of Boycott's and Takahashi's conclusions together with my own.

II. Analysis of Boycott's data.

a. Analytical constants.

b. Frequency distributions.

c. Mean and standard deviation.

d. On the correlation in growth between internodal length and the diameter of the fiber.

III. Takahashi's observation on the length of the internode in different segments of the same frog.

IV. Correlation tables.

I. As my principal object was to find whether there is any definite law relating to the length of the internode and its diameter in different segments of the leg from the same frog, as well as in the same segment of the leg in different sized frogs, I shall not touch many other points discussed by Boycott and especially by Takahashi. Within the range of my examination, I confirm all their findings. Since the evidence of such confirmation will be found in the following pages, I shall present here only the main facts brought out by myself.

1. In a given specimen of *Rana temporaria* (*fusca*) whatever its size, the length of an internode and its diameter are positively correlated, though the correlation is not high; therefore it can be stated that the internodal length varies as the diameter. The degree of correlation increases as the frog becomes larger.

2. When however the lengths of the internodes for given diameters in different sized frogs are compared, the larger frog has for a given diameter longer internodes than the smaller frog. Thus in this case the internode varies according to the relation given by the following general exponential equation

$$y = Ae^{hx}$$

where the constants A and h are to be determined from the observations, y is the internodal length, x the diameter and e the base of the natural system of logarithms.

3. The equation just mentioned expresses also the relation in these two characters in the different segments of the leg from the same frog.

4. Therefore *the rate of the increment of the length of the internode following the increase in the diameter is proportional to the length of the internode itself*, or in mathematical terms.

$$\frac{dy}{dx} = hy$$

This may be considered as the general formula which expresses the relation of the two characters in different segments of the leg of the same frog as well as in corresponding segments from frogs of different sizes.

II. ANALYSIS OF BOYCOTT'S DATA

a. Analytical Constants

For future reference I shall present here the various values of the analytical constants as determined from Boycott's data.

TABLE I
Showing the values in terms of micra of the analytical constants determined from Boycott's data on *Rana temporaria* (*fusca*)

	GROUP I	GROUP II	GROUP III	GROUP IV	GROUP V
No. of measurements	157	1097	1515	605	1916
μ_2 { Diameter	1.7234	1.7785	2.2991	3.3327	3.3265
Internode	1.9359	2.4773	2.6121	5.2862	12.3402
μ_3 { Diameter	-1.1326	-0.1980	-1.5720	-2.6559	-2.7581
Internode	1.2894	3.5331	5.0630	9.4191	30.3224
μ_4 { Diameter	9.7848	8.0596	14.3649	43.5208	32.5211
Internode	19.3369	29.6266	60.1877	110.6646	585.2832
β_1 { Diameter	0.2506	0.0070	0.2034	0.1906	0.2067
Internode	0.2289	0.8212	1.4383	0.6006	0.4893
β_2 { Diameter	3.2944	2.5481	2.7176	3.9184	2.9389
Internode	5.1597	4.8275	8.8212	3.9602	3.8434
K_2 { Diameter	-1.2255	-0.0094	-0.1379	0.1194	-0.2205
Internode	0.0526	0.6267	0.2213	4.3687	1.8820
Skewness { Diameter	-0.2639	-0.0629	-0.3834	-0.1598	-0.3032
Internode	0.1265	0.3473	0.2678	0.3875	0.3463
Mode { Diameter	7.0920	7.6678	9.0207	10.5744	11.1441
Internode	531.9895	669.6903	706.4650	1030.2662	1310.3061
Standard deviation { Diameter	1.3128 $\pm$ 0.0500	1.3336 $\pm$ 0.0192	1.5163 $\pm$ 0.0185	1.8256 $\pm$ 0.0354	1.8239 $\pm$ 0.0198
Correlation { Diameter	139.1366 $\pm$ 5.3071	157.3944 $\pm$ 2.2665	161.6199 $\pm$ 1.9804	229.9173 $\pm$ 4.4604	351.2862 $\pm$ 3.8276
r between { Diameter	.0797 $\pm$ 0.0535	0.1947 $\pm$ 0.0195	0.1480 $\pm$ 0.0169	0.3399 $\pm$ 0.0242	0.3456 $\pm$ 0.0136
Mean { Diameter	6.7475 $\pm$ 0.0707	7.5843 $\pm$ 0.0332	8.4403 $\pm$ 0.0263	10.2826 $\pm$ 0.0501	10.5913 $\pm$ 0.0281
Internode	532.1656 $\pm$ 7.4897	670.2370 $\pm$ 3.2052	706.8977 $\pm$ 2.8007	1031.1571 $\pm$ 6.3043	1311.5344 $\pm$ 5.4131

TABLE 2

Length of internodes. Under each group the first column gives the frequencies when the observed values are reduced to 1000. The second column (F) the observed number of frequencies.

INTER- NODAL LENGTH μ	GROUP I		GROUP II		GROUP III		GROUP IV		GROUP V	
	F.		F.		F.		F.		F.	
150	25.5	4								
250	0	0	1.8	2	0.7	1				
350	114.6	18	14.6	16	11.2	17			0.5	1
450	242.0	38	86.6	95	54.8	83	1.7	1	2.6	5
550	382.2	60	260.7	286	192.1	291	9.9	6	3.1	6
650	152.9	24	278.9	306	264.0	400	29.8	18	6.3	12
750	38.2	6	174.1	191	233.7	354	100.8	61	28.7	55
850	19.1	3	93.9	103	134.0	203	145.5	88	56.9	109
950	19.1	3	54.7	60	66.7	101	216.5	131	90.3	173
1050	6.4	1	19.1	21	29.7	45	175.2	106	104.4	200
1150			11.9	13	6.6	10	122.3	74	131.0	251
1250			2.7	3	2.6	4	67.8	41	101.2	194
1350			0	0	2.0	3	59.5	36	124.7	239
1450			0	0	0	0	31.4	19	81.9	157
1550			0	0	0.7	1	16.5	10	73.1	140
1650			0.9	1	0	0	13.2	8	59.0	113
1750					0	0	6.6	4	47.0	90
1850					0	0	1.7	1	30.3	58
1950					0.7	1	0	0	22.4	43
2050					0.7	1	1.7	1	12.0	23
2150									5.7	11
2250									7.8	15
2350									4.7	9
2450									0.5	1
2550									1.6	3
2650									3.1	6
2750									0	0
2850									1.0	2
		157		1097		1515		605		1916

TABLE 3

Diameter of internodes. Under each group the first column gives frequencies when the observed values are reduced to 1000. The second column (F) the observed number of frequencies.

DIAMETER μ	GROUP I		GROUP II		GROUP III		GROUP IV		GROUP V	
		F.		F.		F.		F.		F.
3	6.4	1			0.7	1	5.0	3	0.5	1
4	12.7	2	6.4	7	4.6	7	0.0	0	0.5	1
5	146.5	23	62.0	68	37.6	57	1.7	1	4.7	9
6	286.6	45	140.4	154	70.0	106	24.8	15	11.0	21
7	305.7	48	263.5	289	163.0	247	59.5	36	50.1	96
8	146.5	23	289.9	318	206.6	313	39.7	24	78.3	150
9	44.6	7	138.6	152	194.7	295	124.0	75	82.5	158
10	51.0	8	96.6	106	298.4	452	343.8	208	264.6	507
11			2.7	3	13.2	20	143.8	87	137.8	264
12					9.2	14	148.8	90	226.0	433
13					2.0	3	76.0	46	114.8	220
14							28.1	17	25.6	49
15							5.0	3	3.7	7
		157		1097		1515		605		1916

b. Frequency Distributions. Chart I

An examination of the polygons which represent the observed data shows clearly that they deviate from the normal symmetrical figures to a considerable extent. Even those curves which come nearer to the symmetrical figure have the maximum ordinates too high to be fitted with the equation of the normal curve

$$y = \frac{a}{\sigma \sqrt{2\pi}} e^{-\frac{x^2}{2\sigma^2}}$$

An actual determination of the various constants from the data according to Pearson's method of the moment proves the correctness of our supposition, for in every case the values of β_1 and skewness deviate widely from zero, while in the normal symmetrical curve, these constants just mentioned should equal zero or be very near to it, and in addition the value of β_2 is not equal to 3.

When we classify our curves according to the corresponding values of the constants, the frequency distributions of the diameters should be represented by Pearson's curve of type 1, except in group 4, in which it will be represented by the curve of type 4.

On the other hand, the frequency distributions of the length of the internode in groups 1, 2 and 3 will be represented by the curve of type 4, while the remaining two groups are represented by the curve of type 6.

I have not calculated the theoretical values of the curves, since the observed curves as they are answer our present purpose. In plotting these curves, we reduced the total frequency on the basis of one thousand in each case. This not only renders a comparison easier, but at the same time we can get a clear notion as to the mode of a gradual transformation from small to larger values where the total number of the internodes is approximately constant throughout life (see p. 28 for the validity of this assumption).

Thus we assume that there are one thousand internodes in the nerve of the thigh, and these numbers are distributed in different stages of the growing period in the manner shown in figs. 1 (diameter) and 2 (internode).

Let us first examine the curves for the internode. In group 1 (see p. 24) the curve is much nearer to the symmetrical figure and the range of the length of the internodes extends only from 150 to 1050 micra. We notice here that the theoretical maximum ordinate corresponds with the internodal length of 532 micra; that is it stands nearly at the middle of the abscissa.

In group 2 we notice several changes when compared with the curve for group 1.

1. The total range of the variates has been increased and extended more towards the higher values (250 to 1650 micra).

2. The position of the node has moved from 532 in group 1, to 670 micra in group 2, and thus it is now situated at about one-third of the distance of the total range from the lower end.

3. Finally the shape of the curve shows a still greater deviation from the symmetry.

All these changes when compared with group 1 indicate that as a consequence of the growth of the frog, the internodes have grown in length, and therefore the shorter internodes which are so frequent in group 1, have become less frequent in this group.

With some insignificant modifications, the same statements apply to all the other curves. Finally in group 5 we see a very wide extension of variates from 350 to 2650 micra, and at the same time the ranges found in group 1 can only be found in this case in the lower third of the total range. The position of the mode has now moved from 532 to 1310 micra, indicating that as a whole, the modal value of the internode has increased 146 per cent when compared with group 1. From being nearly symmetrical, the curve itself has become highly skew. The increase in range of the variates may also be shown from the successive values of the standard deviation which increase gradually in round numbers from 139 micra in group 1 to 351 micra in group 5.

Let us examine now the curves for the diameters. For this character the distributions of the frequencies are very irregular as compared with the curves which illustrate the distributions of frequencies of the internodes.

Nevertheless in all fundamental features, the two records agree very nicely; that is the range of variates is smaller in group 1 than in group 5. The position of the mode moves gradually from a less diameter to a greater diameter; from 7 to 11 micra. The position of the entire curve moves from left to right. The only distinct difference which can be found in the curves of the internode and diameter lies in the fact that the total amount of increment during these five successive stages is considerably less in the latter than in the former, and in fact the internodes show almost three times as much increase as the diameters (see p. 28) and consequently the changes in the form of the curves for diameter from group 1 to group 5 is less conspicuous than in the case of the internode.

c. Mean and Standard Deviation

As has already been pointed out by both Boycott and Takahashi, a determination of the proper average is very difficult on account of possible modifications due to the technique. The larger the animal, the longer is the internode, and vice versa. In the former case, the longer internode is easily broken and as a consequence the shorter internodes are more often measured than the longer ones, while in the smaller frogs such accidents are less frequent, and the resulting mean will therefore be much nearer to the true value in this case than in the case of the larger frogs. We cannot however eliminate this error but it must be kept in mind when we come to draw the final conclusions. Our observations yield the following mean values for each group:

		GROUP I %	GROUP II % inc.	GROUP III % inc.	GROUP IV % inc.	GROUP V % inc.
Mean	Diameter . . .	6.70.0	7.612.43	8.425.15	10.352.43	10.657.01
	Internode . . .	532.20.06	70.225.94	706.930.95	1031.293.76	1311.5146.45

As we should expect, the mean values for both diameter and internode increase from group 1 to group 5. In order to see how much increase both diameter and internode have made during these five stages, the two measurements in group 1 were compared with those of the succeeding stages. As is shown in the same table, the percentage increase for the diameter is far below that for the internode. In fact the total increment in the diameter of group 5 over that of group 1 is only slightly more than half of the value of group 1, while in the case of the internode, it amounts to more than one and a half times the value of group 1. This means of course that the internode has grown three times more rapidly than the diameter during the same period. Whether or not this relation of growth is also true for the growth of the thigh itself, when its width and length are compared, is an interesting point to be determined. At least one fact is true as will be shown later, that the growth rates of the internode and of the entire nerve are approximately equal.

As to the constancy of the number of internodes on a nerve fiber, I may quote first the view of Boycott from his original paper. Boycott says (p. 377):

It appears from the figures that there is a small increase in the number of internodes during the growth in the length of the nerve. The increase is small, yet it is regularly progressive. It may be due to ordinary errors of experiment, while on the other hand it may represent an increase which actually takes place. There is one special circumstance which renders it suspicious. This is the fact that the longer an internode the less likely is it to remain unbroken and capable of being traced throughout its length: the longer internodes will in this way not be measured as often as they should, and hence the average internodal length will be smaller than it should be proportionately to the increase in the length of the internodes. This would account for the increase which is seen in the table, but whether it is the whole explanation it is impossible to say. Assuming that the figures are in the main correct, it must be concluded that there is a small (and somewhat doubtful) increase in the number of internodes, though the main part of the total increase in length is due to an increase in the length of individual internodes.

In the summary he says again (p. 380):

The number of internodes thus remains approximately constant at all ages. There is a small increase in the total observed number; there are however reasons for thinking that this is due to errors of method.

This question of constancy in the number of internodes in the nerve cannot easily be decided until we have a strong reason to believe that the average value obtained for the internode from the given nerve is nearly correct. There is still another theoretical objection to considering the observed values as the average of the whole population, when a small fraction of the lower end of the nerve only is examined (see p. 40). I have also tested this main point by using mean values obtained by the present biometric method, and the following are the results.

TABLE 4

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5
Sciatic length in mm.....	16.25	21.07	25.60	34.10	48.17
Mean internodal length in μ	532.2	670.2	706.9	1031.2	1311.5
Number of internodes.....	30.53	31.43	36.21	33.07	36.73
Percentage increase.....		2.94	18.60	8.32	20.31

When the figures given above are considered, they show a gradual increase in the number of internodes as the nerves grow longer, the significance of which depends of course on the correctness of the mean values. This method of treatment is crude however, owing to the fact that the observed length of the internode for any given diameter differs more or less from the theoretical value. There are some reasons to believe that the theoretical are preferable to raw mean values for this determination. When we employ the theoretical values of the length of the internodes, the results are as follows:

TABLE 5

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5
Theoretical length of the internode.....	531.8	678.8	684.4	988.7	1360.6
Number of nodes.....	30.56	31.04	37.40	34.50	35.40
Percentage increase.....	0	1.57	22.38	12.89	15.83

From the foregoing we see that whether we use the raw mean length or the corrected mean length, the results are approximately the same; that is the data show an increase in the number of the internodes as the nerve becomes longer. In fact the total gain in the number of the internodes, when group 1 is compared with group 5, amounts to as much as 16 per cent. Even if we assume that the total number of measurements in group 1 was too small (157 observations) to trust its validity, the difference between group 2 (1097 observations) and group 5 amounts to as high as 14 per cent.

We can test this conclusion still another way; since the percentage increase in the internodal length when the mean length in group 1 is compared with that of group 5, is approximately 150 per cent, while the gain in the length of nerve runs as high as 200 per cent, thus the length of the nerve increases faster than that of the internode.

In this connection it is a matter of interest to note that the average number of the internodes is 33.8 in the present case, while Boycott has obtained 34.5. Although the present method of obtaining the mean values was entirely different from that used by Boycott, nevertheless the results show a difference of less than 1.5 per cent, indicating a close agreement between the simpler and more complicated treatment. Therefore we are forced to conclude as Boycott did, that so far as our present data are concerned, the number of the internodes increases with the advancing ages of the frogs.

It is however extremely important before drawing any final conclusions from these data to consider at least the two following points:

1. Technical difficulty in measuring the longer internodes as often as the shorter. This has been already discussed.
2. Number of newly added fibers.

This is certainly an important point to be considered.

Takahashi commented on this point thus:

It follows from the foregoing result that so long as the nerve receives new (young) fibers, there will always be internodes which are relatively short, since they belong to fibers which have been subjected to the lengthening process for only a short time. The presence of these fibers reduces the average length of the internodes, and hence accounts in part at least for Boycott's observation that on the average the lengthening of the internodes in the sciatic nerve is slightly less than that of the nerve itself.

Both these points require further study.

d. *On the Correlation in Growth Between the Internodal Length and Diameter*

It has been stated by the previous investigators that the length of the internode varies with the diameter of the fiber in the sense that the fibers of greater diameter have the longer internodes. According to Birge ('82) during growth the average diameter of the fibers in the frog increases, and the average internodal length also becomes greater. In general, the results just mentioned are in harmony with the findings of Boycott and Takahashi. In this connection however, Boycott has drawn attention to an important point. He stated that

an examination of the table will show however that *the internodal length increases proportionately more than the diameter*, so that in a large frog, the length of the internodes in the fiber of given diameter, is greater than in a small frog (p. 372).

Later Takahashi advanced this conclusion of Boycott a step further stating that

in the same frog, *the length of the internodes* at different levels on fiber of like diameter in the nerves to the leg, *increases towards the periphery*. This increase appears to be associated with the more rapid growth of the distal segments of the leg, but the influence of the segment on the portion of the nerve within it, is less marked as the frogs become larger.

Thus Boycott's and Takahashi's investigations reveal that the relation between diameter and internodes is far more complicated than it was considered to be by the earlier investigators, and varies not only when the different sized frogs are compared, but also at the different levels in the leg of the same frog.

I shall discuss this problem under two heads:

1. The correlation of the length and diameter of the internode from a single locality in a given frog.
2. The relation between the length of the internode and its diameter.
 - a. From a single locality in frogs of different sizes.
 - b. In the different segments of the leg of the same frog.

1. CORRELATION OF THE LENGTH AND DIAMETER OF THE INTERNODE FROM A SINGLE LOCALITY IN A GIVEN FROG }

In order to see whether or not the length of the internode is correlated with the diameter, I have determined the coefficient of correlation between the two characters just mentioned in each group from the formula given below

$$r = \left(\frac{\sum x' y'}{n} - v' v'' \right) \frac{1}{\sigma_1 \sigma_2}$$

(see Davenport's Statistical Methods, 1904) and obtained the following results:

	GROUP 1	GROUP 2	GROUP 3	GROUP 4	GROUP 5
Coefficient of correlation or $r =$	.0797 $\pm$.0535	0.1947 $\pm$.0195	0.1480 $\pm$.0169	.3399 $\pm$.0042	.3456 $\pm$.0136

In every case the coefficient of correlation is positive and is greater than the corresponding probable error. We therefore consider that the diameter and the length of the internode are certainly correlated. Though the degree of correlation is never high, nevertheless we can say positively that so far as the present data are concerned, the longer internode is associated with larger diameter in the values given in each group, and vice versa.

We also noticed in the above table that in general the degree of correlation becomes greater as the animal becomes larger. In another trial we have obtained from Takahasi's data (measurements from sciatic in thigh only) a coefficient of correlation as high as 0.6681, his observations having been made on large frogs (body weight 26 to 63 grams). Since during the period of rapid growth the relation between the two characters must be more irregular, it follows that the degree of correlation would be less in the young than in the adult. Therefore the view maintained by the earlier investigators that "the length of the internodes

varies with the diameter of the fiber in the sense that the fibers of greater diameter have the longer internodes" is correct when the fibers are from the same segment of the same animal.

This conclusion is still true even when all the measurements in the five groups are added together, since in this case again the greater diameter is still associated with the longer internode, though the degree of correlation is lessened.

The average of the coefficients of correlation in the five groups is found to be 0.2216.

2. THE RELATION BETWEEN THE INTERNODAL LENGTH AND DIAMETER

a. From a Single Locality in Frogs of Different Sizes

We have shown already that the diameter varies with the internodal length in the same animal (this is true either for an individual or for averages of several individuals) though the degree of correlation is not high.

When however, several frogs of different sizes are compared with each other, the internodal length varies, as has been found by Boycott, proportionately more than the diameter, so that in a large frog the length of the internodes on a fiber of given diameter is greater than in a small frog. This finding of Boycott can plainly be seen when one examines either the tables or charts of his original paper. I have also prepared by a different method the tables and charts to demonstrate this point.

The following table shows the observed values of the internodal lengths corresponding to the different values of diameters in all of the five groups of Boycott. These values have been determined from the correlation tables (see tables 10-14, pp. 45-47) the internodal length being the means of arrays corresponding to the various values of the diameter.

TABLE 6

DIAMETER μ	GROUP 1 μ	GROUP 2 μ	GROUP 3 μ	GROUP 4 μ	GROUP 5 μ
3	450	—	350	517	550
4	150	579	536	—	950
5	515	571	561	750	728
6	521	608	606	870	1055
7	558	683	655	900	1039
8	541	698	724	892	1123
9	464	705	718	941	1200
10	625	660	759	1025	1306
11		817	750	1090	1373
12			757	1129	1384
13			617	1113	1420
14				1068	1523
15				1050	1993

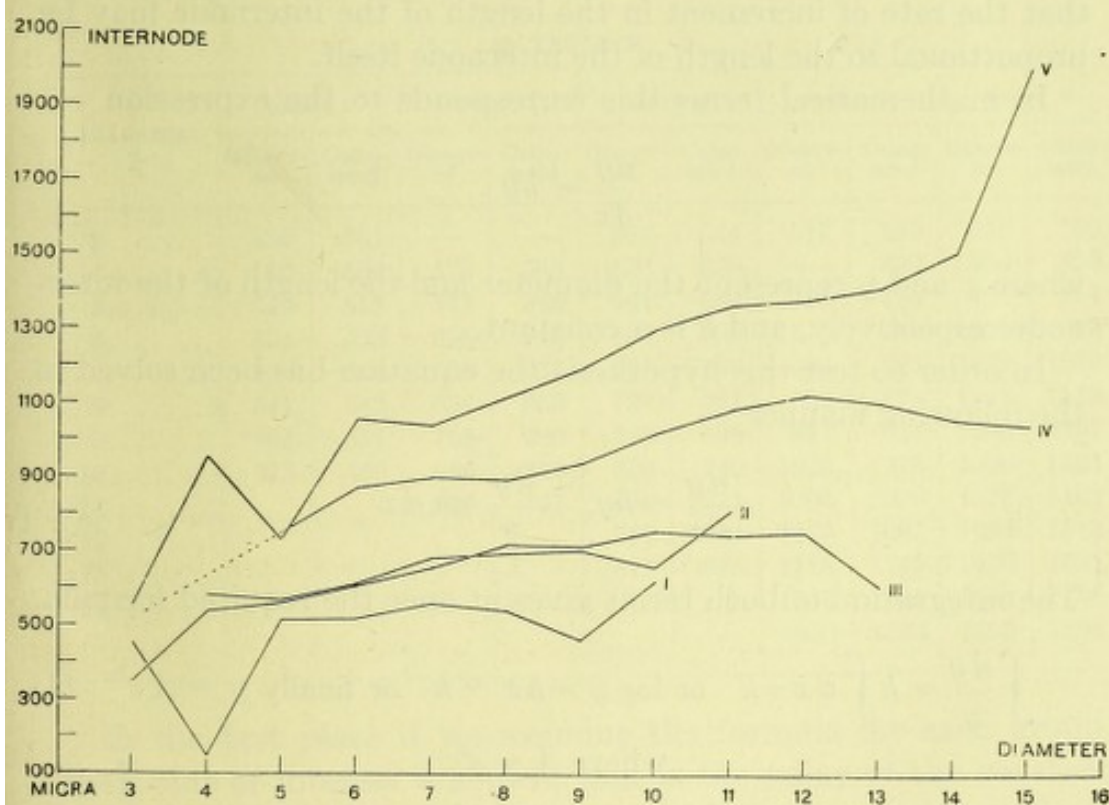


CHART 2. Showing the observed values of the internodal lengths corresponding to the different values of the diameters in all of the five groups of Boycott.

Let us first examine the curves (see chart 2). Although the curves are irregular at the ends where the number of observations is not large, yet each can be seen to follow a characteristic course when the middle portion is examined. We notice, as Boycott found, that the length of the internode varies proportionately more than the diameter, since the length of the internode becomes longer for a given diameter as the frogs become larger. In addition these curves are not parallel to one another but diverge more from the curve of group 1 as the frog becomes larger. This divergence in the course of the curves would of course mean that the relative amount of the increment to the internode following to the increase in diameter is not equal, but is greater for the larger frog than for the smaller frog. Since the smaller frog has a shorter internode for a given diameter than in the larger frog, it follows that the longer internode gains in increment proportionately more than the shorter internode. This relation suggests that the rate of increment in the length of the internode may be proportional to the length of the internode itself.

In mathematical terms this corresponds to the expression

$$\frac{dy}{dx} = hy$$

where x and y represent the diameter and the length of the internode respectively, and h is a constant.

In order to test this hypothesis the equation has been solved in the following manner:—

$$\frac{dy}{dx} = hy, \quad \frac{dy}{y} = h dx$$

The integration of both terms gives at once the required formula.

$$\int \frac{dy}{y} = h \int dx + k \quad \text{or} \quad \log y = hx + k \quad \text{or finally} \quad y = A e^{hx} \quad (1)$$

$$\text{where } A = e^k.$$

Therefore if our hypothesis is correct, the foregoing exponential equation should adequately express the relation between the

length of the internode and its diameter in frogs of any given size.

Assuming that our hypothesis is correct, the next step was the actual determination of the two constants h and A from the observations for each group. I have determined these constants by ordinary algebraic methods, and the five equations stand as follows:

TABLE 7

For group 1.....	$y = 477.6 e^{.0159x}$
For group 2.....	$y = 501.1 e^{.0400x}$
For group 3.....	$y = 470.2 e^{.0426x}$
For group 4.....	$y = 559.9 e^{.0553x}$
For group 5.....	$y = 613.5 e^{.0752x}$

The following table (8) shows the values of the observed and calculated length of the internodes corresponding to the various values of the diameter. The calculations have been made for each group by the formulas just given.

TABLE 8

DIAMETER μ	GROUP I		GROUP II		GROUP III		GROUP IV		GROUP V	
	Observed	Calculated	Observed	Calculated	Observed	Calculated	Observed	Calculated	Observed	Calculated
3	450	501	—	—	350	534	517	660	550	769
4.....	150	509	579	565	536	558	—	699	950	829
5.....	515	518	571	588	561	582	750	738	728	894
6.....	521	525	608	612	606	607	870	780	1055	963
7.....	558	533	683	637	655	639	900	825	1039	1039
8	541	542	698	663	724	661	892	871	1123	1118
9.....	464	551	705	690	718	690	941	921	1200	1207
10.....	625	560	660	718	759	720	1025	973	1306	1301
11.....			817	747	750	751	1090	1029	1373	1403
12.....					757	784	1129	1087	1384	1513
13.....					617	818	1113	1149	1420	1631
14.....							1068	1215	1523	1758
15.....							1050	1283	1993	1896

In the first place if we examine the formula for each group, one point of interest is shown, that is the value of the constant " h " which determines the steepness of the curve (see formula 1) increases regularly from the smaller to the larger frog. Since,

when the value of this constant is equal to zero, the resulting curve will be parallel to the abscissa with the distance corresponding to the value of the constant A , therefore the increase in the constant " h " means that the curve becomes steeper as the frog becomes larger, at the same time with an increasing distance of the entire curve from the base line. For the latter statement we find one exception in group 3, in which the value of the constant " A " is smaller than that of the smallest frog. If however we examine the observed mean values in that group, a peculiarity can be found at once; that is the mean values in both the lower and upper ends of the curve are too small compared with the values found in the middle. Since our determination of the constants is based on the observations, such an aberrant result for this particular group is inevitable. Nevertheless, the higher value of the other constant " h " indicates a higher probability that all the mean values for group 3 should have been greater than they actually were.

Therefore with a single exception in the one constant in group 3, the equations are in harmony with the general feature in the growth of the internodes. When we come to an actual test, the observed values are too irregular to make valuable a detailed comparison with the corresponding values obtained by the equation.

On account of the difficulty just mentioned, the question of fit between the theoretical values and the observed can best be judged by an actual comparison of the two graphical representations of the values (see chart 3).

As we notice from the curves, the fit of the theoretical curve to the observed is very satisfactory in the first three groups, and the continuous lines run about the middle of the observed points. In groups 4 and 5 it is not as good as in the former three groups, nevertheless when the irregularity of the observed values in these two groups is considered, the continuous lines should be regarded as the best approximation to the observed values. At least the continuous lines run very close to the observation in the best part of the curve, that is the middle portion where the number of observations is large.

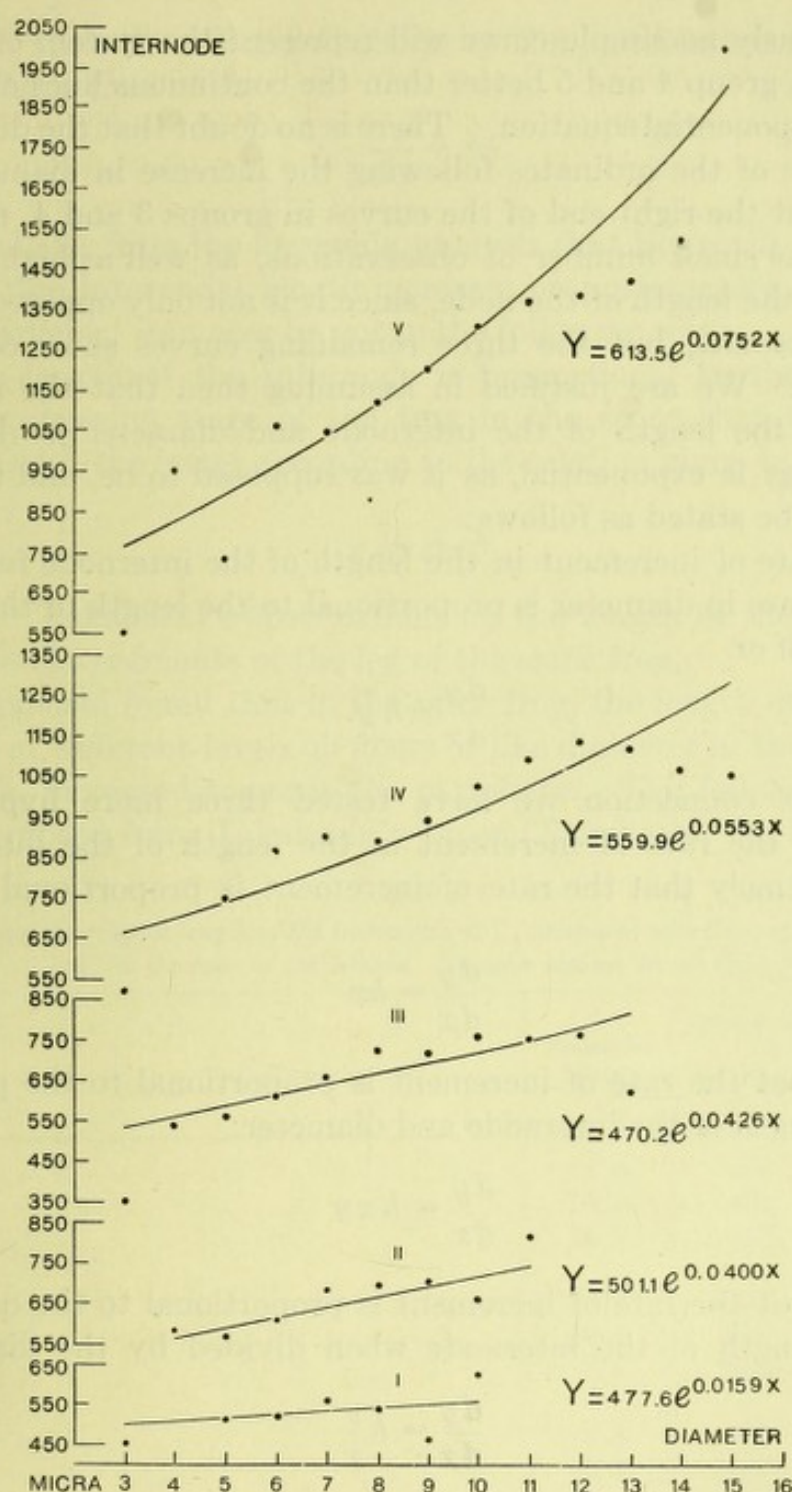


CHART 3. Showing the theoretical and observed values for the length of the internodes in all the five groups. The dots show the observed mean values, and the continuous lines the theoretical values as calculated by the formulas in table.

Obviously no simple curve will represent the system of points shown in group 4 and 5 better than the continuous lines obtained by the exponential equation. There is no doubt that the diminishing value of the ordinates following the increase in diameter, to be seen at the right end of the curves in groups 3 and 4, must be due to the small number of observations, as well as high irregularity in the length of the node, since it is not only opposed to the general results, but the three remaining curves show contrary relations. We are justified in assuming then that the relation between the length of the internode and diameter in different sized frogs is exponential, as it was supposed to be, and the law can now be stated as follows:

The rate of increment in the length of the internode following the increase in diameter is proportional to the length of the internode itself or

$$\frac{dy}{dx} = h y.$$

In this connection we have tested three more hypotheses touching the rate of increment in the length of the internode.

1. Namely that the rate of increment is proportional to the diameter:

$$\frac{dy}{dx} = h x$$

2. That the rate of increment is proportional to the product of the length of the internode and diameter:

$$\frac{dy}{dx} = h x y$$

3. That the rate of increment is proportional to the quotient of the length of the internode when divided by the diameter:

$$\frac{dy}{dx} = h \frac{y}{x}$$

When however these three equations were tested, it was found that so far as the constants are to be determined from the observations, all these equations give a very poor fit to the observed

data. Thus there is no doubt as to the justification of our first hypothesis that

$$\frac{dy}{dx} = hy$$

It follows from the foregoing analysis that Boycott's conclusion that "the internodal length increases proportionately more than the diameter" can now be put in the following way:

The length of the internode is proportional to the diameter in any growing stage of the frog in the sense that the former varies with the latter according to the relation given by the equation

$$y = A e^{hx} \quad (1)$$

III. Takahashi's observations on the length of the internode in different segments of the leg of the same frog.

Takahashi found that in the same frog, the length of the internodes at different levels on fibers of like diameter in the nerves to the leg, increased towards the periphery. The following is the table quoted from Takahashi's paper (Takahashi '08, table 8):

TABLE 9

Showing the relative length of the internodes at T_3 compared with those at S_1 , as a standard, in the case of the several diameter classes in all three frogs

	DIAMETER IN μ	LENGTH OF INTERNODES IN μ AT	
		S_1	T_3
Frog 3.....	4.0	425	578
	5.3	530	714
	6.3	578	805
Frog 5.....	5.3	623	834
	6.3	645	917
	7.3	805	1039
Frog 8.....	5.3	711	837
	6.3	828	963
	7.3	885	1001
Averages.....	5.9	659	855

The above table shows clearly that for any given diameter the length of the internodes which are nearer to the proximal end of the leg are shorter than those away from it. This observation suggests the possible existence of an exponential relation between the internodes from different segments of the leg in the same frog. In order to investigate this point, the total averages were taken as shown in the above table. I took this average for the reason that first, all frogs are mature, and second, on account of higher variability of the length of the internode, the sum of the larger number is important. From the average we see that the diameter which is approximately 6 micra gives 659 micra for the internode at the upper end of the thigh, and 855 micra for the internode found at the upper portion of the foot (cruro-tarsal joint), that is the relation between the two is 1:1.29.

To determine whether or not a similar relation can also be found between the length and diameter of the internode in different sized frogs, I selected two values of the internode for the diameter of 6 micra; one from group 4 and the other from group 5, as these two mean lengths are the nearest values giving a diameter comparable with the averaged figures in Takahashi's table. We have here 780 micra and 963 micra for the internodes in groups 4 and 5 respectively.² In this case the proportion between the two internodes is 1 : 1.23 as contrasted with 1 : 1.29 in the other.

These two ratios agree very well for the diameter of 6 micra. This agreement is necessary for the argument, but does not permit us to conclude that the relation between the diameter and the length of the internode in the different segments of the leg of the same frog is also exponential, since we cannot determine the form of the curve. For this reason we must seek for further evidence.

An examination of the figs. 3 to 6 in Takahashi's paper gives us an additional reason for the above conclusion, since there we find that not only the length of the internode for a given diameter increases towards the periphery, but the three lines repre-

² Takahashi has pointed out that the internodes on the fibers from the American frog, *R. pipiens*, are shorter than those found by Boycott on the fibers of *R. temporaria* (*fusca*).

senting the diameters of 5.3, 6.3 and 7.3 micra respectively are not parallel, but show a slight divergence (see also Takahashi '08, tables 4 to 8). The amount of divergence is very slight, but is regularly greater for the line corresponding to the greater diameter. This relation agrees with that found to exist between the two characters in the frogs of different sizes. We feel justified therefore in concluding that our hypothesis that the relation between the diameter and the length of the internode is exponential, even when applied to the length of the internodes from the different segments of the leg of the same frog, is correct.

On the basis of the preceding argument, we present the following final conclusion:—The exponential equation

$$y = A e^{hx}$$

expresses the relation between the length of the internode and its diameter either in different segments of the leg of the same frog, or in frogs of different sizes. This law seems applicable to both *Rana pipiens* and *Rana temporaria* (*fusca*).

Thus far we have merely demonstrated that when the data are examined, the relation existing between the two characters under consideration is adequately expressed by an exponential formula, but we do not make any inference as to the immediate factors which bring the two characters during the growth period into such exponential relation. As one of the factors, Takahashi counts the segmental influence, by which I understand the elongation of the internodes of Ranvier depend on the elongation of the segments of the limb in which they are found.

If this view of Takahashi is correct, we shall be justified in concluding that the growth of the segments in *Rana pipiens* follows also an exponential formula. Although unfortunately I have not sufficient data to test this point just mentioned in either *Rana pipiens* or *Rana temporaria*, I find it to be true at least in the case of the leg of the toad as shown by the recent investigation of Kellicott on *Bufo lentiginosus* (1907) in which the rate of increment in the length of the segments is proportional to the length of the segment itself.

This relation has been determined from the coefficients of correlation and standard deviation given in his paper. We assumed of course that the regression between the body length and length of thigh, shank and foot is linear. This is admittedly a crude method, nevertheless so far as we wish at the present moment to determine the general features of the curves, such simple treatment answers the purpose.

We have however one important difference between the segments of *Rana* and those of *Bufo*, in the fact that in *Rana* the length of the segment regularly increases towards the periphery, while in *Bufo*, the length of the shank is least and that of the thigh and of the foot stand in the order named. Thus in the toad if the growth of the internodes is not at all influenced by the elongation of the segments, we shall find a progressive increase in the length of the internodes towards the periphery, and the exponential law in this case will apply to the entire extent of the leg, while on the other hand if the segmental influence is the main determining factor, we shall find the shortest mean length of the internode in the shank, and the exponential law in this case will be applicable to each segment independently.

Therefore the question of general segmental influence as the main determining factor of the length of the internode in the different segments, can best be tested from the internodes in the nerve of the different segments in the leg of the toad. I hope to be able to take up this question in the near future.

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CORRELATION TABLES.

TABLE 10

Showing correlation of length and diameter of internodes in micra

GROUP I

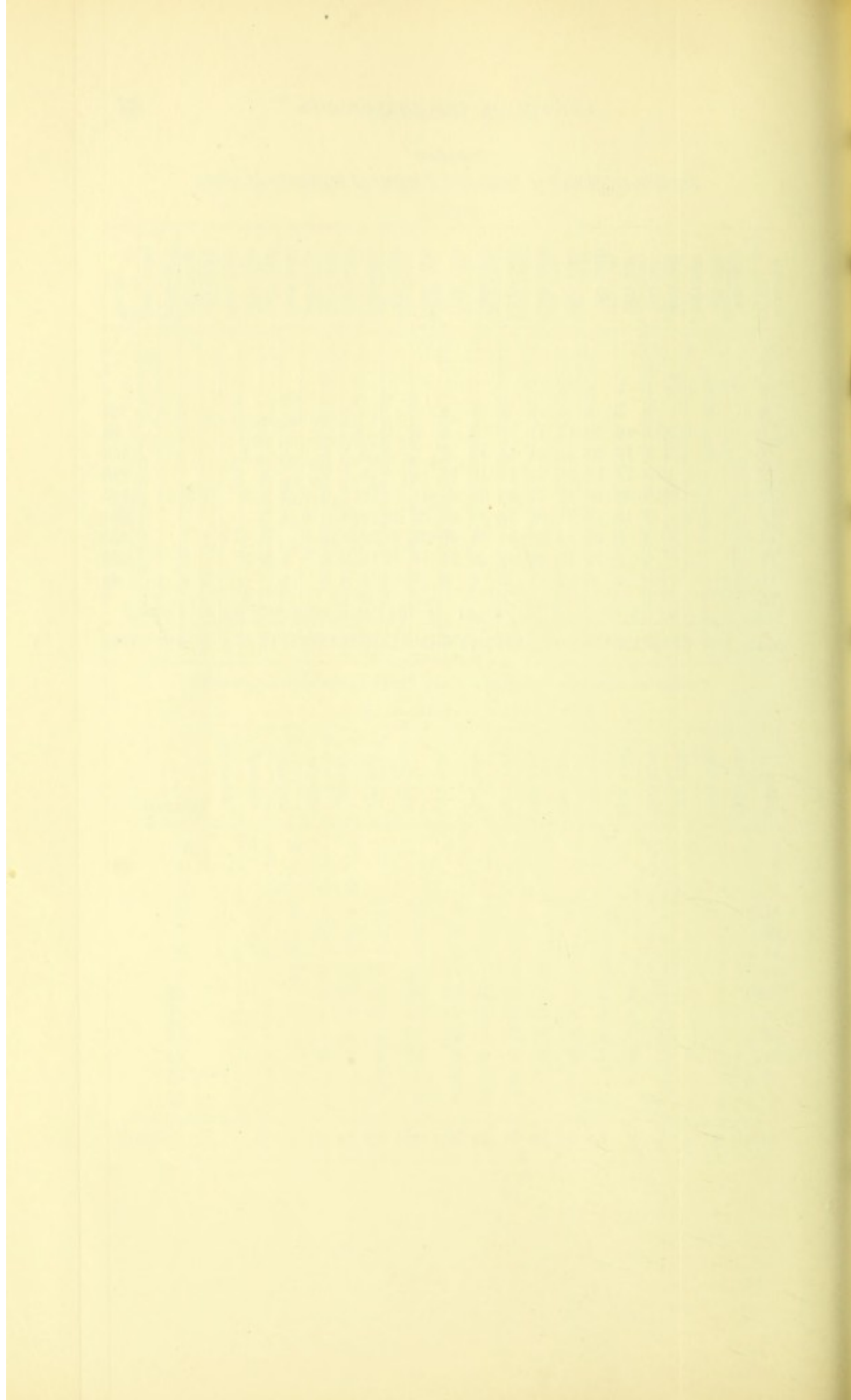
Diameter	Internode	100-200 μ	200-300	300-400	400-500	500-600	600-700	700-800	800-900	900-1000	1000-1100	Totals
3 μ					1							1
4.....	2											2
5.....				3	7	9	3	1				23
6.....	1			7	12	15	8			1	1	45
7.....				4	8	23	8	3	2			48
8.....	1			3	3	10	3	2		1		23
9.....					6	1						7
10.....				1	1	2	2		1	1		8
Totals.....		4	0	18	38	60	24	6	3	3	1	157

TABLE 11

Showing correlation of length and diameter of internodes in micra

GROUP II

Diameter	Internode	200-300 μ	300-400	400-500	500-600	600-700	700-800	800-900	900-1000	1000-1100	1100-1200	1200-1300	1300-1400	1400-1500	1500-1600	1600-1700	Totals
4 μ			1	2	2			2									7
5			4	20	18	15	7	3	1								68
6			2	30	59	32	15	9	6							1	154
7			4	18	71	85	53	33	11	9	5						289
8			5	13	68	106	57	31	22	7	6	3					318
9	1			7	39	30	37	18	14	5	1						152
10	1			5	29	37	22	6	5		1						106
11						1		1	1								3
Totals		2	16	95	286	306	191	103	60	21	13	3	0	0	0	1	1097



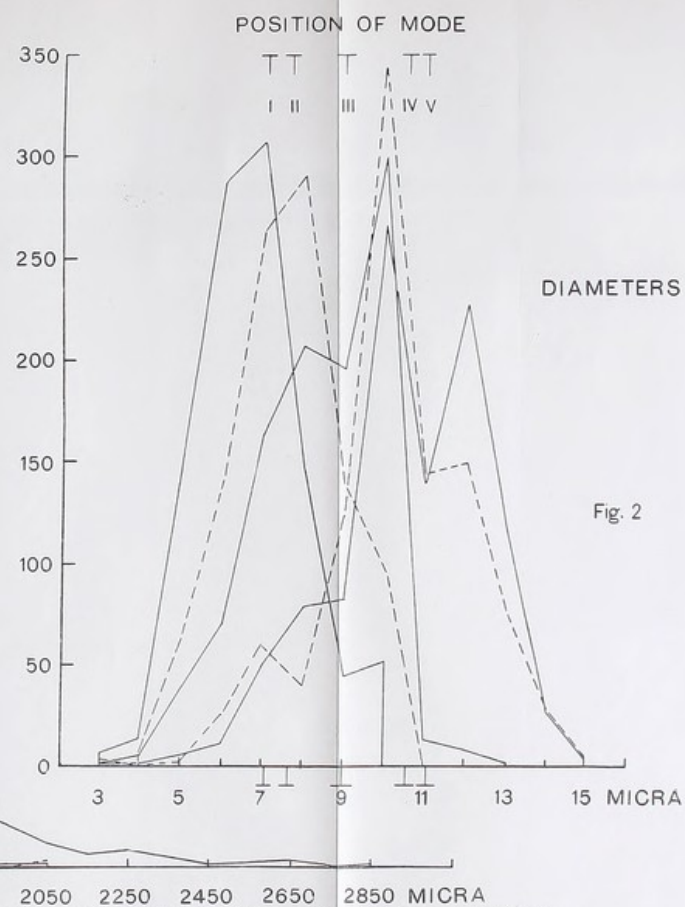
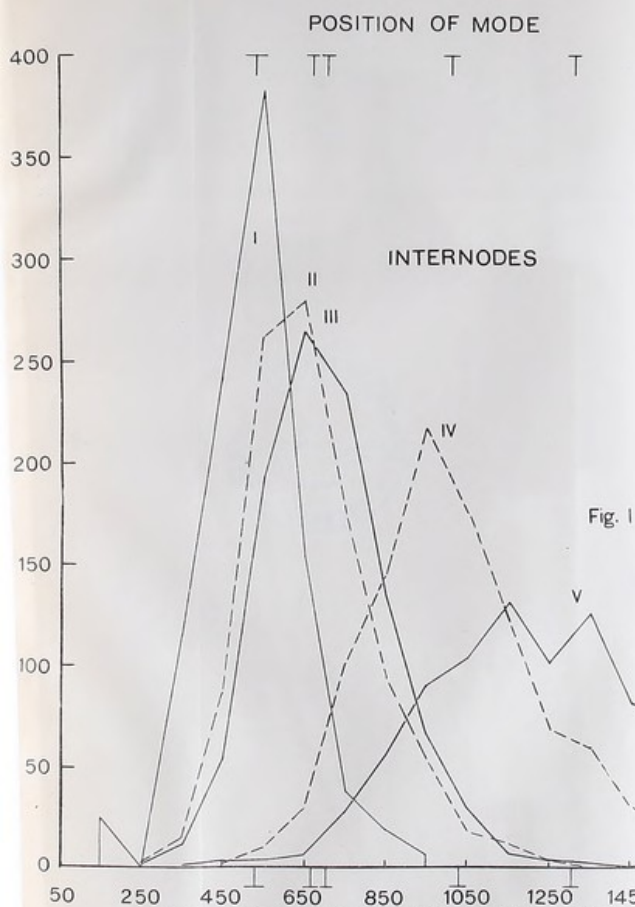


CHART 1. Curves showing the distribution of frequencies of the several lengths of the internodes and diameters for all of the five groups. Fig. 1, Internodes. Fig. 2, Diameters.